

A NEW ACTINOLEPID ARTHRODIRE FROM THE LOWER DEVONIAN OF ARCTIC CANADA

by D. L. DINELEY and LIU YUHAI

ABSTRACT. Actinolepid material from the lower Devonian of Prince of Wales Island, Arctic Canada, described as *Eskimaspis heintzi* gen. et sp. nov. closely resembles *Kujdanowiaspis* and *Heightingtonaspis*, especially in the pattern of the head shield. In comparison with *Baringaspis* which is associated with it, it differs mainly in the short nuchal plate and the ornamentation of scattered tubercles.

THE actinolepid arthrodires from the lower Devonian of Arctic Canada were first given palaeontological description by Miles in 1973, at which time *B. dineleyi* was established. Afterwards, a large amount of actinolepid material was collected in the same area by members of the Department of Geology, University of Bristol, in the summer of 1973. Recently, when we prepared this collection a distinct new form, *E. heintzi* gen. et sp. nov. associated with *B. dineleyi* was found. Meanwhile the new material suggests that some specimens designated as *B. dineleyi* by Miles in his description belong to *E. heintzi* too. The main purpose of the present paper is to give *E. heintzi* a brief description. Thus, only details of *B. dineleyi* not previously known are given here.

With the exception of the complete head shields, the remains consist mainly of disarticulated plates together with a few partial trunk shields. Most of the photographs included below are of the rubber casts following negative preparation with dilute hydrochloric acid.

The arthrodires occur in the Upper Member of the Peel Sound Formation at three localities: locality A at the bank of Porolepis Brook (= Miles's localities D + H); (Miles 1973, fig. 1); locality B at the bank of Forsyth Brook, about 1.5 km south of Baring Channel and 4.5 km west of locality A; locality C at the bank of Ermine Creek about 2 km south of locality A (text-fig. 1). The material is housed in the collections of the Palaeobiology Division of the Canadian National Museum of Natural Sciences, Ottawa, and bears National Museum catalogue numbers, prefixed NMC.

DESCRIPTION

Order EUARTHRODIRA
Suborder DOLICOTHORACI
Family ACTINOLEPIDIDAE
Eskimaspis gen. nov.

Etymology. After *Eskimo*, the aboriginal of the Canadian Arctic.

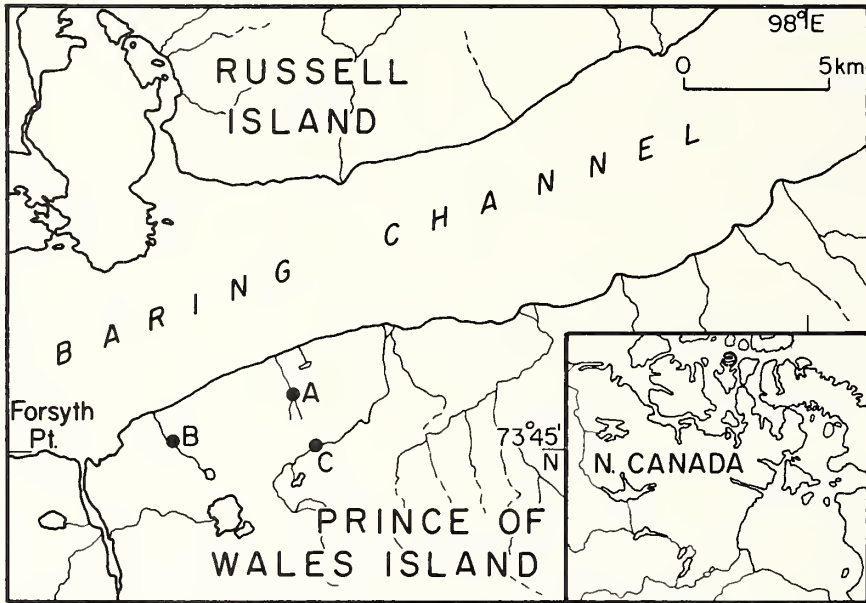
Diagnosis. An actinolepid arthrodire with narrow preorbital region, broad but short nuchal plate, wide paranuchals and broad anteriorly tapering straight-sided central plates, posterior dorsolateral plates deep, anterior lateral plates low, longer than high; ornamentation of scattered tubercles.

E. heintzi sp. nov.

Etymology. Species is named in honour of the late Professor A. Heintz.

Diagnosis. As for the genus.

Holotype. A nearly complete head shield with the counterpart, c. NMC 34101a and 34101b.



TEXT-FIG. 1. Southern coastal margin of Baring Channel, Prince of Wales Island, N.W.T., Canada, showing vertebrate-bearing localities in the Peel Sound Formation.

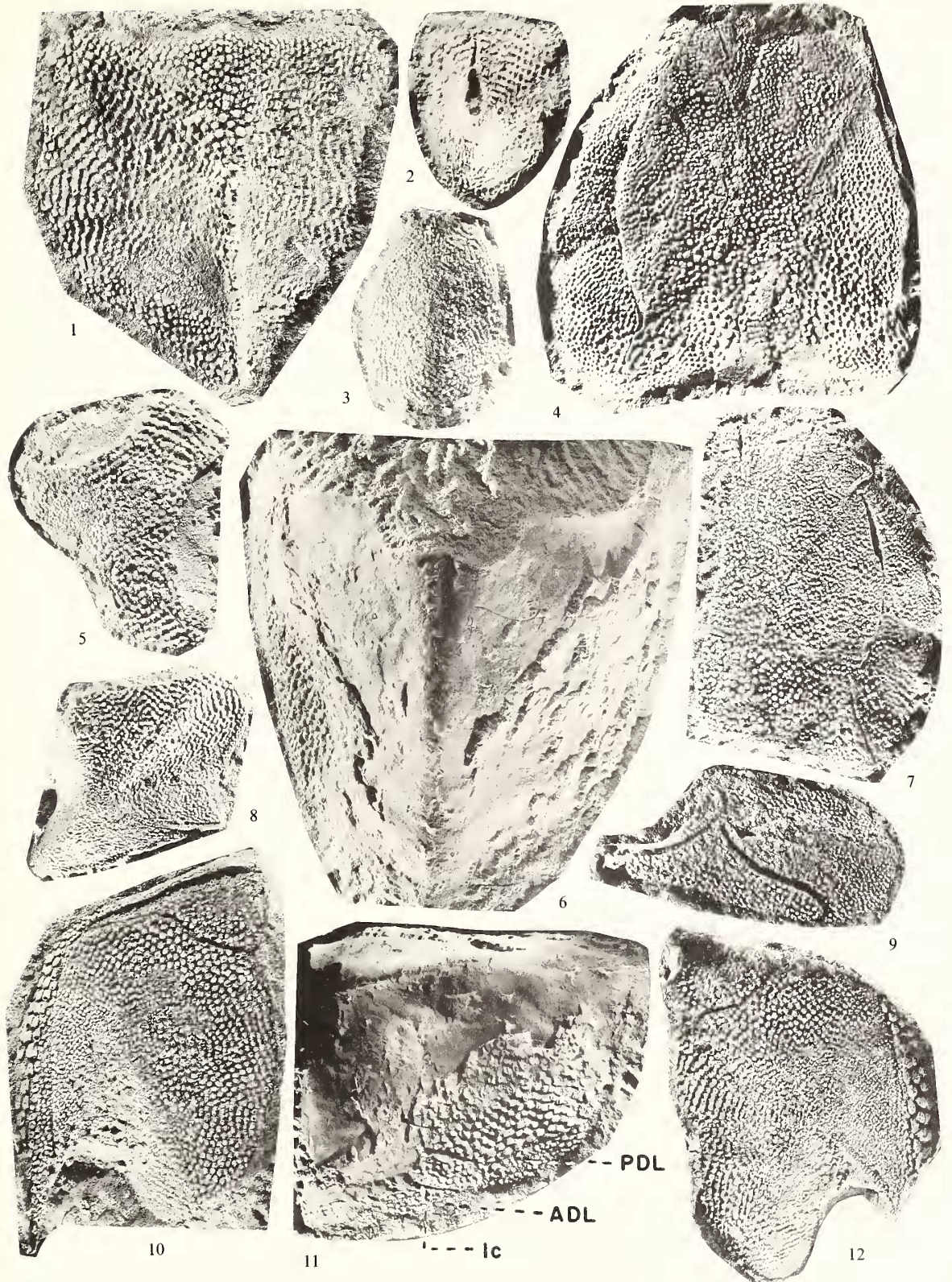
Locality. Early Devonian, Peel Sound Formation; Prince of Wales Island, Arctic Canada.

Description. Head shield (Pl. 79, figs. 4, 7; Pl. 80, fig. 5; text-figs. 2, 3A). At least six head shields are available. They are almost all the same in size, and the type is 43 mm in length excluding the rostral capsule. The roof is rather broad; despite the loss of the postmarginal plates its width is 52 mm crossing the antero-lateral corner of the paranuchal plate each side. The head shield has a typical outline of a dolichothoracan, with a moderate concavity for the reception of the separate rostral capsule, a quite narrow preorbital part in which the orbital notches are shallow but distinct. The lateral margins of the shield are smooth and regular, while the embayments for the postmarginal plates are shallow.

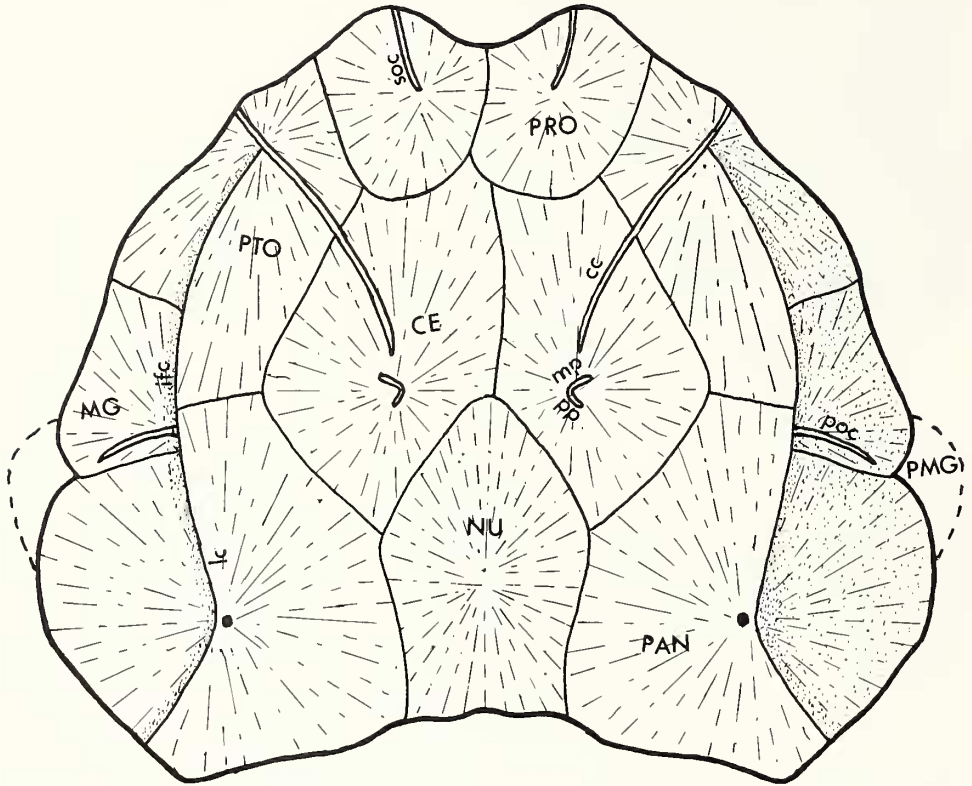
Owing to the complete fusion of the plates of the head shield, the sutures between them can be traced in only a few specimens. Closely comparing with *Kujdanowiaspis* and *Heightingtonaspis* (White 1969, figs. 29–32; text-figs. 3C, D this paper) the new form has a moderately long, five-sided nuchal plate which is with its pointed anterior end wedged between the posterior parts of the paired central plates. As that in *Kujdanowiaspis*, *Heightingtonaspis*, *Sigaspis* (Goujet 1973, fig. 3B) and *Baringaspis* (Miles 1973, fig. 2; text-fig. 3B this paper), the mesial margin of the marginal plate in *Eskimaspis* lies in the path of the main infraorbital sensory line. Nevertheless *Eskimaspis* is

EXPLANATION OF PLATE 79

Figs. 1–12. *Eskimaspis heintzi* gen. et sp. nov. 1, median dorsal plate, cast of 34120, locality A; $\times 1.5$. 2, posterior dorsal plate, type B, cast of 34119, locality A; $\times 2$. 3, posterior dorsal plate, type A, cast of 34118, locality A; $\times 2$. 4, head shield, cast of 34101, locality C; $\times 1.5$. 5, right posterior ventro-lateral plate, cast of 34116, locality A; $\times 1.5$. 6, median dorsal, anterior and posterior dorso-lateral plates, cast of 34117, locality A; $\times 1.5$. 7, head shield, cast of 34105, locality A; $\times 1.5$. 8, left anterior lateral plate, cast of 34113, locality C; $\times 1.5$. 9, left suborbital plate, cast of 34108, locality A; $\times 2$. 10, right intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34125, locality A; $\times 1.5$. 11, median dorsal, anterior and posterior dorso-lateral plates, cast of 34117, locality A; $\times 1.4$. ADL, anterior dorso-lateral plate; PDL, posterior dorso-lateral plate; Lc, main lateral line. 12, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34138, locality A; $\times 1.5$.



DINELEY and LIU, lower Devonian arthropod



TEXT-FIG. 2. *Eskimaspis heintzi* gen. et sp. nov. Head shield in dorsal view, restored after holotype 34101, locality C; $\times 2$. CE, central; MG, marginal; NU, nuchal; PAN, paranuchal; PMG, postmarginal; PRO, preorbital; PTO, postorbital; cc, central canal; ifc, infraorbital canal; lc, main lateral line; mp, middle pit line; poc, preopercular canal; pp, posterior pit line; soc, supraorbital canal.

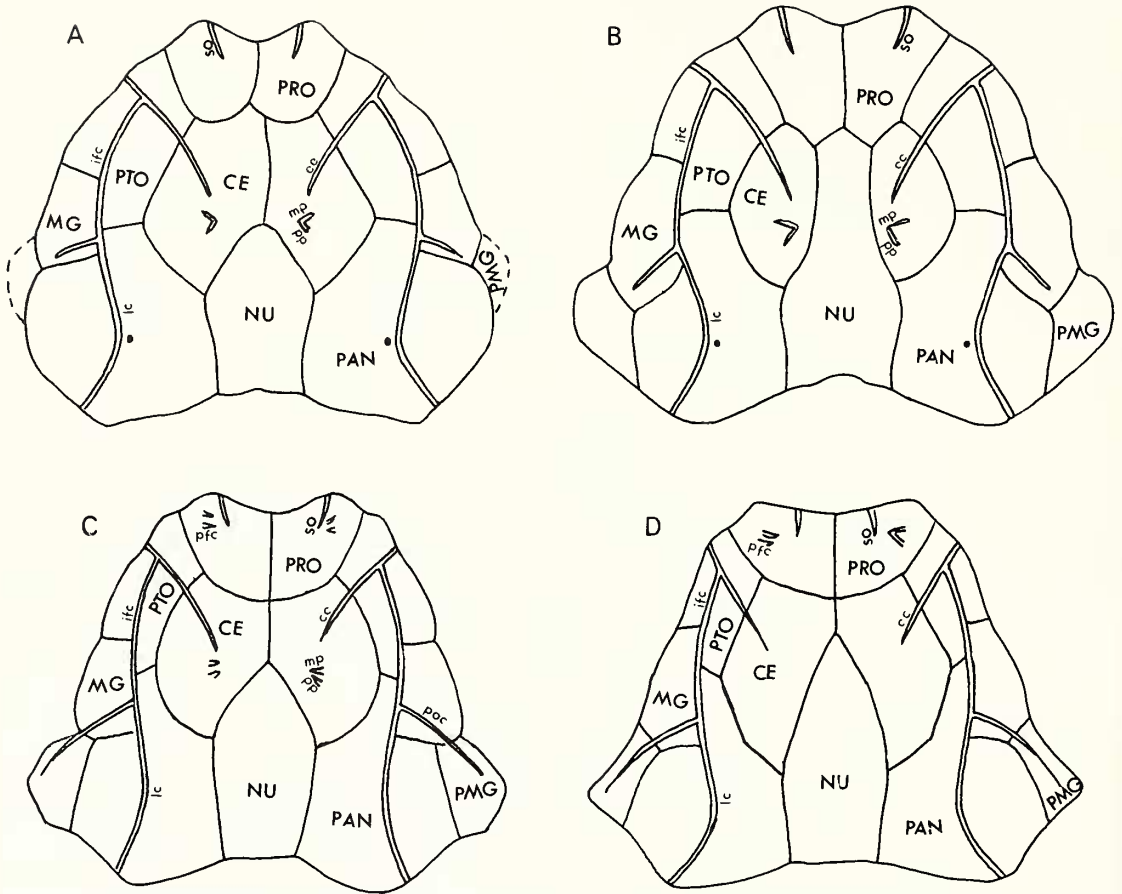
EXPLANATION OF PLATE 80

Figs. 2, 4-7, 9, 11-12. *Eskimaspis heintzi* gen. et sp. nov. 2, left posterior dorso-lateral plate, cast of 34110, locality A; $\times 2$. 4, left posterior ventro-lateral plate, 34111, locality C; $\times 1.5$. 5, head shield, cast of 34106, locality A; $\times 1.5$. 6, anterior dorso-lateral plate, cast of 34102, locality C; $\times 2$. 7, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34114, locality C; $\times 1.5$. d.l, dorsal lamina of intero-lateral plate. 9, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34126, locality B; $\times 1.5$. 11, arctolepida indet., right infragnathal, medial view, 34129, locality C; $\times 2$. 12, posterior medio-ventral plate, cast of 34139, locality A; $\times 1.5$.

Figs. 1, 3, 8, 10, 13. *Baringaspis dineleyi* Miles. 1, right intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, 34127, locality A; $\times 1.5$. 3, left intero-lateral, anterior ventro-lateral, anterior ventral, and spinal plates, cast of 34128, locality B; $\times 1.5$. 8, anterior medio-ventral plate, cast of 34143, locality A; $\times 1.6$. 10, posterior medio-ventral plate, cast of 34133, locality A; $\times 1.3$. 13, right posterior dorso-lateral plate, cast of 34135, locality A; $\times 2$.



DINELEY and LIU, lower Devonian arthropods



TEXT-FIG. 3. Head shields. A, *Eskimaspis heintzi* gen. et sp. nov., restored after 34101; $\times 1.2$. B, *Baringaspis dineleyi* Miles, after Miles 1973, fig. 2; $\times 1.2$. C, *Kujdanowiaspis* sp., modified from White 1969, fig. 30; $\times 0.9$. D, *Heightingtonaspis anglica* (Traquair), modified from White 1961, fig. 31; $\times 0.9$. CE, central; MG, marginal; NU, nuchal; PAN, paranuchal; PMG, postmarginal; PRO, preorbital; PTO, postorbital; cc, central canal; ifc, infraorbital canal; ic, main lateral line; mp, middle pit line; pfc, profundus canal; poc, preopercular canal; pp, posterior pit line; so, supraorbital canal.

distinguished from *Kujdanowiaspis* and *Heightingtonaspis* in detail, such as the proportionally larger width of the shield, the shorter nuchal, the broader paranuchals, and the finer tubercles.

The sensory lines of the head shield are arranged as in the other dolicho thoracans. However, the middle and posterior pit-lines, not usually seen in this group, display clearly at the termination of the supraorbital lines. Besides, the foramina of the endolymphatic ducts occurs at the top of the bend of the main infraorbital lines on the paranuchal plates in both specimens NMC 34104 and 34101.

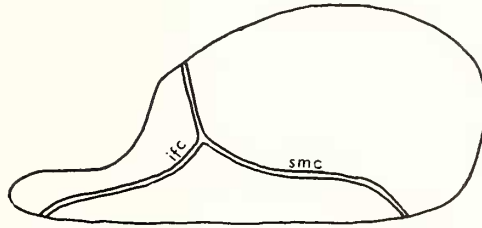
The ornamentation of the head shield consists of scattered tubercles, which in some parts, such as the paranuchal plates, have locally a linear arrangement or a tendency to concentric rows. The finer tubercles are crowded and lack regular distribution, while the larger ones are, on the whole, settled in the nuchal and mesial parts of the paranuchals as well as along some sutures.

As described above, *Eskimaspis* is distinguished from *Baringaspis* in the nuchal, paranuchal, and central plates. On the other hand, the tubercular ornamentation of *Eskimaspis* is different from the ridged one of

Baringaspis. This fact is important for our determination of the detached plates of both genera, which so far are always found together in Prince of Wales Island.

The visceral surface of the head shield is ill-disclosed in NMC 34016 (Pl. 80, fig. 5). The posterior margin of the shield is not thickened and is without the glenoid fossae for the articulation with the trochleae of the trunk armour. Of the endocranium only the occipital part is incompletely revealed. It emphasizes the similarity between the *Eskimaspis* and *Kujdanowiaspis*.

Cheek plate. The suborbital plates (Pl. 79, fig. 9; text-fig. 4), which are quite common in the collection, are the only cheek plates to be determined. They are as those described by Miles (Miles 1973, p. 112, pl. 13, fig. 2; pl. 14, fig. 5). On the basis of the tubercular ornamentation the suborbital plates both in the collection and as described by Miles, should belong to *Eskimaspis*, therefore, for the description of the plates readers are referred to Miles's paper. Surprisingly, in the great volume of the collections there has up to now been no suborbital plate determined as that of *Baringaspis*.



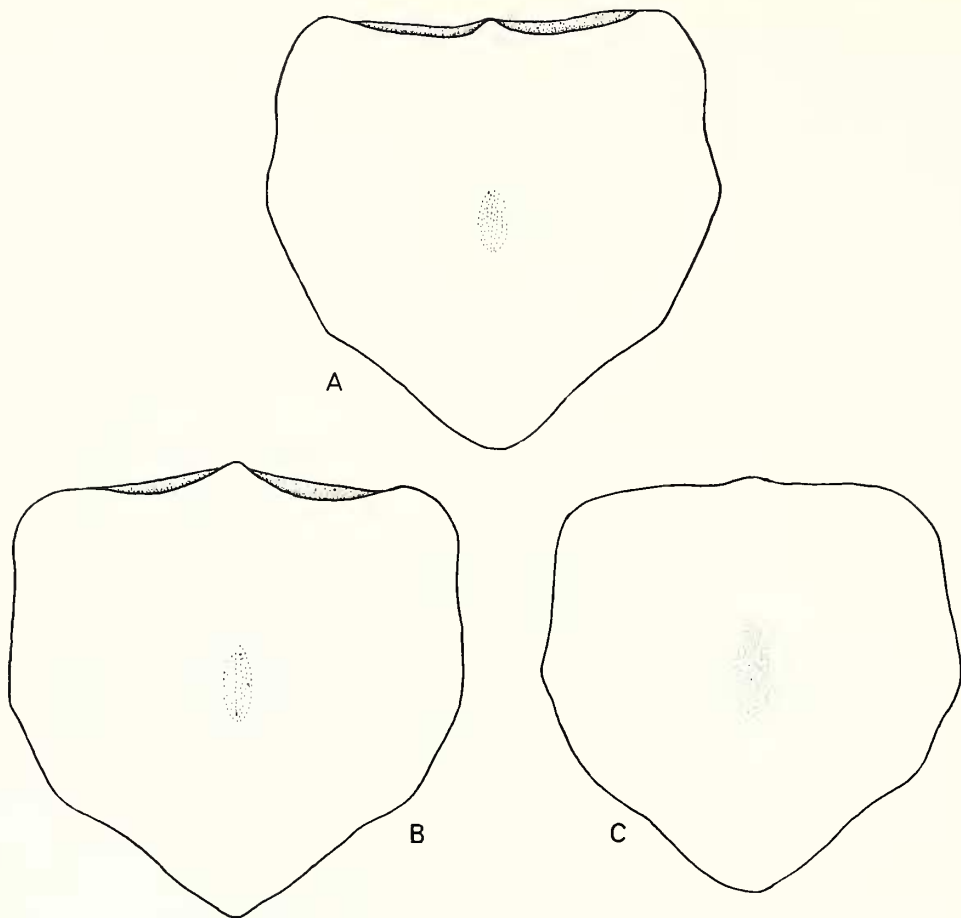
TEXT-FIG. 4. *Eskimaspis heintzi* gen. et sp. nov., left suborbital plate, after cast of 13226, unrecorded locality of Prince of Wales Island, in Miles 1973, Pl. 14, fig. 5; $\times 1.6$. ifc, infraorbital canal; smc, supra-maxillary canal.

Jaws. A lower jaw (Pl. 80, fig. 11) in the collection is for convenience described here; because of the lack of association it cannot be with certainty determined to belong to *Eskimaspis* or *Baringaspis*. It is exposed from medial side and bends towards the midline near its anterior end. The posterior end seems to be broken. On the dorsal face the bone curves slightly antero-posteriorly and in the posterior part nine small teeth can be seen, of which the anterior three have broken away. Further forward, the dorsal face is smooth without any teeth for about one-third of the length of the bone. At the very anterior end three large teeth are set. The transverse section of one broken tooth shows that the tooth is compact, without pulp cavity. Though the lower jaw cannot be examined in detail, comparing it with those of *Phlyctaenaspis* (Heintz 1935, pl. 11, figs. 3-4) and that of an actinolepid from the Water Canyon Formation of Utah (Denison 1958, fig. 101F) it is more similar to the latter.

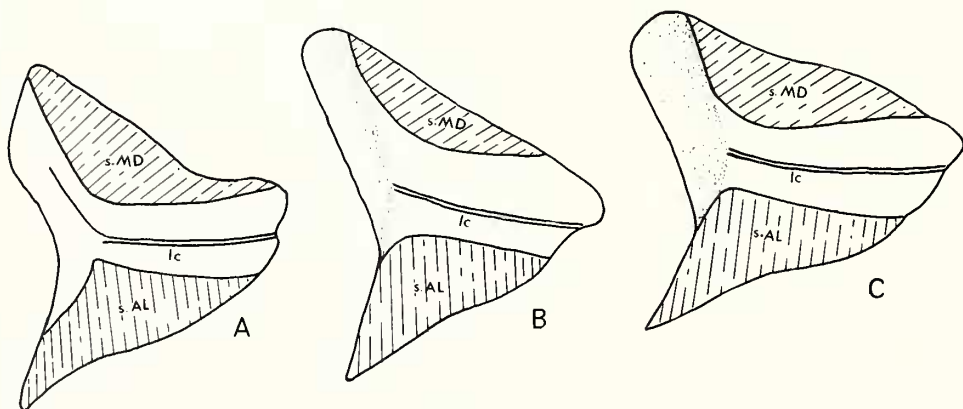
Trunk plates. Most plates of the trunk armour are detached, but some median dorsal plates are articulated with anterior dorsal-lateral plates, and with fragments of the posterior dorsal-lateral plates as well. As is the usual case in other dolichothoracans, the plates of the antero-lateral part of the ventral wall of the trunk armour are always associated as a unit.

The dorsal median plate (Pl. 79, figs. 1, 6, 11; text-fig. 5A) is typical actinolepid, short and broad (Denison 1958, pp. 515-518). In NMC 34120 it is 40 mm in length, 44 mm in width crossing the lateral angles. On the dorsal surface a median crest runs in the posterior half of the plate, while a pair of unornamented areas display along the anterior margin on both sides of the anterior median process of the plate. A posterior median lobe is developed as in most actinolepids. On the ventral surface a weak median crest has arisen (Pl. 79, fig. 11) which is interrupted to give two or three pieces in some specimens. The tubercles of the ornamentation are set in concentric rows except in the triangular area from the tip of the median crest to both anterior lateral angles of the plate where they are scattered and lack regular arrangement.

The anterior dorsal-lateral plate (Pl. 80, fig. 6; text-fig. 6A) has no trochlea for the articulation with the head shield. The ornamented surface is low, with a projection of the posterior margin dorsal to the lateral line. In this aspect the plate is similar to that of *Bryantolepis* (Denison 1958; text-fig. 108H) as well as *Baringaspis* (text-fig. 6B). The lateral line runs parallel to the edge of the overlap area for the median dorsal plate. The tubercles of the ornamentation are crowded and tend to rows parallel to the lateral line.



TEXT-FIG. 5. Median dorsal plates. A, *Eskinaspis heintzi* gen. et sp. nov., after 34120, locality A; $\times 1.5$. B, *Baringaspis dineleyi* Miles, restored after cast of 13264, in Miles 1973, pl. 15, fig. 4. C, *Kujdanowiaspis* sp., after Denison 1958, fig. 107I; $\times 1.6$.

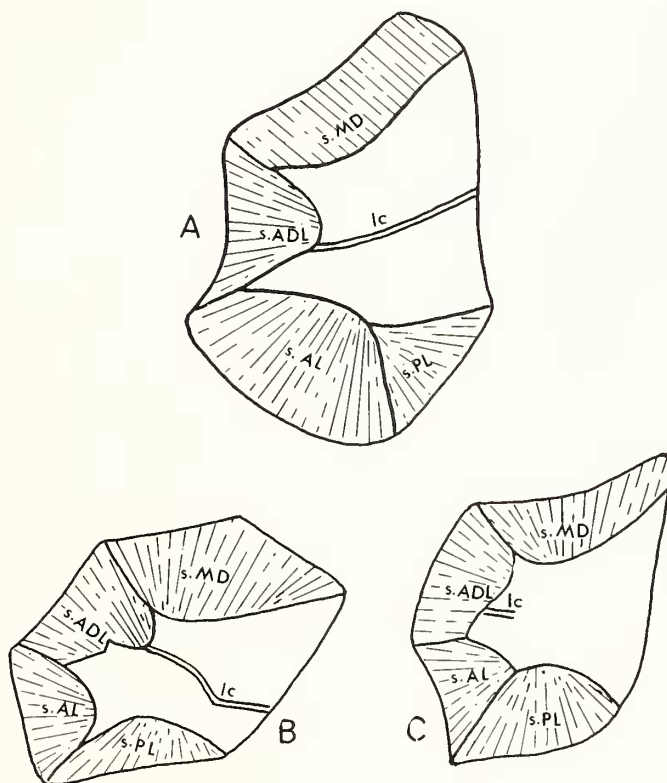


TEXT-FIG. 6. Left anterior dorso-lateral plates. A, *Kujdanowiaspis* sp. after Denison 1958, fig. 108I; $\times 1.7$. B, *Baringaspis dineleyi* Miles, restored after cast of 13263, in Miles 1973, pl. 4, fig. 1; $\times 2.4$. C, *Eskinaspis heintzi* gen. et sp. nov., restored after cast of 34102, locality C; $\times 2.2$. lc, main lateral line; s.AL, s.Md, overlap areas for anterior lateral and median dorsal.

The posterior dorsal-lateral plate (Pl. 80, fig. 9) is quite deep with wide overlap areas for the adjacent plates. The plate compares with that of *Bryantolepis* (Denison 1958, fig. 109H) and *Kujdanowiaspis* (Denison 1958, fig. 109I) in having an ornamented surface deep posteriorly and shallow anteriorly. It is unique in that the overlap area for the anterior lateral plate is strikingly large. To a great extent, therefore, the ornamented surface may be constricted ventrally by the overlap area of the anterior lateral plate, instead of the posterior lateral plate as in most actinolepids (Denison 1958, fig. 109). A longitudinal ridge divides the plate nearly equally. Part of the lateral line runs across the plate just under the ridge, and continues on the corresponding part of the anterior dorsal-lateral plate at an angle parallel to the lateral angle of the median dorsal plate (Pl. 80, fig. 11). The ornamentation consists partly of tubercles and partly of ridges.

A posterior dorsal-lateral plate of *Baringaspis dineleyi* occurring in this collection shows that it is shallower than that of *Eskimaspis* (both in overall proportion and in the ornamented surface alone), and like most actinolepids it has a moderate overlap area for the anterior lateral plate. The exposed surface is ornamented with lines of tubercles. The lateral sensory line crossing the plate is curved (Pl. 80, fig. 13; text-fig. 7B).

The anterior lateral plate (Pl. 79, fig. 8; text-fig. 8A), closely comparable with that of *Heightingtonaspis* (White 1969, fig. 22) and *Baringaspis* (Miles 1973, fig. 4), is little more than a parallelogram with the posterior dorsal corner rounded. But it differs from both genera in that the length is greater than the height. The focal-point from where the faint ridges dividing the plate into quadrants radiate is antero-ventral to the topographic centre of the plate. The anterior quadrant with very fine tubercles is inflected into an apron. A moderate embayment for the pectoral fenestra occurs in the posterior quadrant, which is roughly equal to the upper one in size. On the whole,



TEXT-FIG. 7. Left posterior dorso-lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34110, locality A; $\times 2.2$. B, *Baringaspis dineleyi* Miles, after cast of 34135, locality A; $\times 2$. C, *Kujdanowiaspis* sp., after Denison 1958, fig. 109I; $\times 1.5$. lc, main lateral line; s.ADL, s.AL, s.MD, s.PL, overlap areas for anterior dorso-lateral, anterior lateral, median dorsal, posterior lateral.

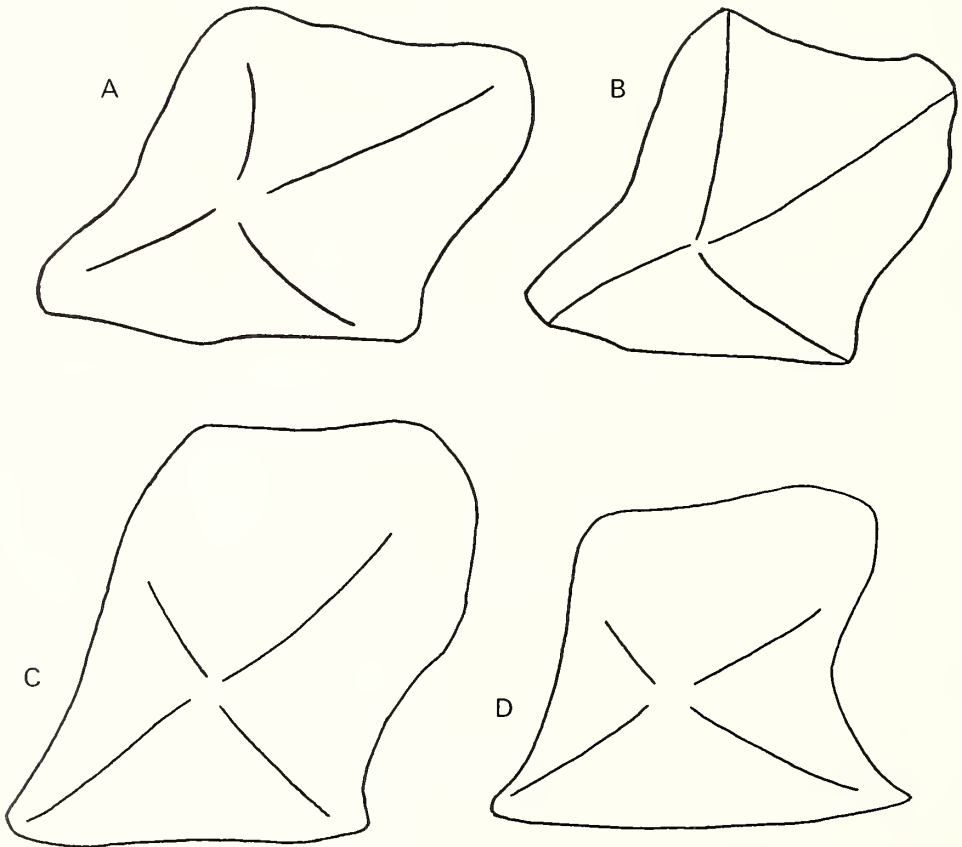
the nearer to the focal-point the tubercles of the ornamentation are, the finer they are. Meanwhile the tubercles are sometimes fused into disjointed rows.

The posterior lateral plate has not yet been determined.

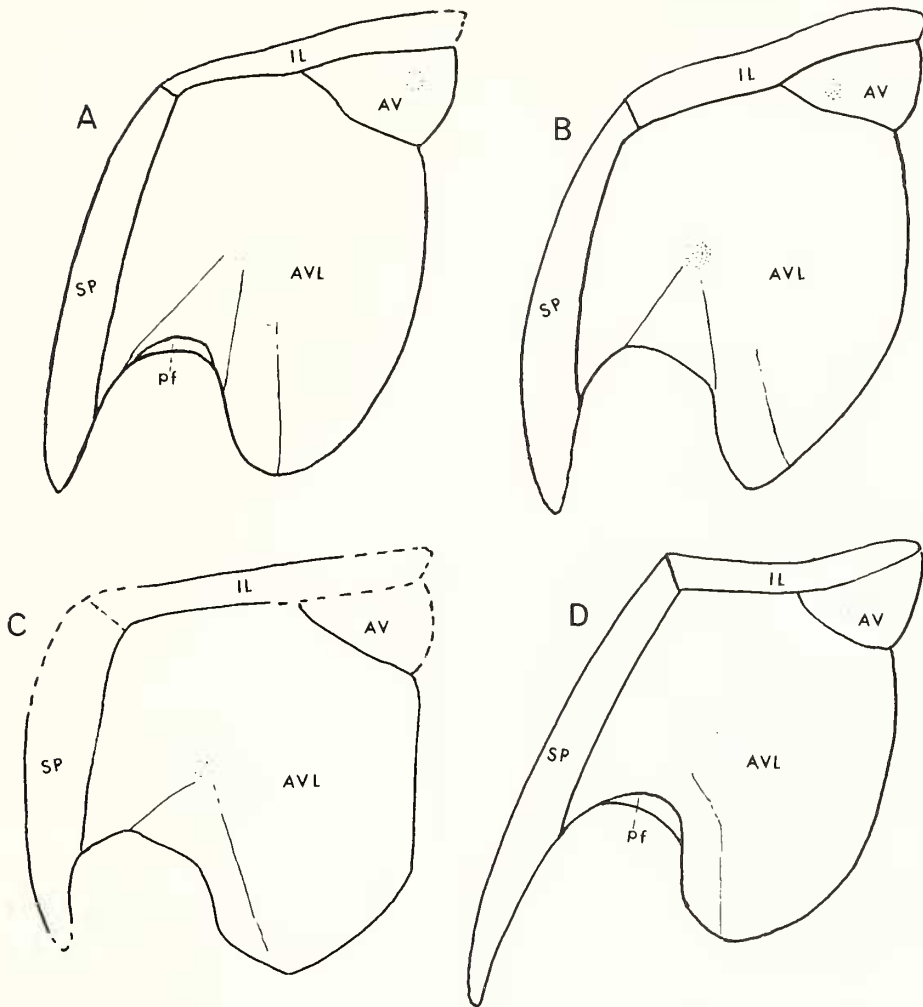
The ventral wall of the trunk armour with its pair of anterior ventral plates is of normal actinolepid type. On the whole, it is similar to that of *Baringaspis* disregarding the ornamentation.

The intero-lateral plate (Pl. 79, figs. 10, 12; Pl. 80, figs. 1, 3; text-fig. 9A) is identical to the pattern in most dolicho thoracans. Its ventral lamina is narrow, ornamented with scattered tubercles, which are as fine as those of the anterior quadrant of the anterior lateral plate. The dorsal lamina is not commonly preserved in the group but occurs in NMC 34114 d.1 (Pl. 80, fig. 7). It seems to be strongly infolded even allowing for distortion. The lamina is deeper and more uniform than in other genera. In contrast with that of the well-known genera of the group, it is remarkable for having a smooth surface without any ornamentation.

The anterior ventro-lateral plate and spinal plate are both similar to those of *Kujdanowiaspis* (Denison 1958, fig. 112H) and *Baringaspis* (Pl. 80, fig. 1; text-fig. 9B). The anterior ventro-lateral plate is relatively uniform owing to the less convex median margin and the moderate extension of the spinal margin in the posterolateral direction. A deep and narrow pectoral sinus occurs between the anterior ventro-lateral and spinal plates. The latter terminates level with, or over, the posterior margin of the anterior ventro-lateral plate. In some specimens the pectoral fenestra is displayed in counterpart. It is comparatively small, situated just at the top of the pectoral sinus and faces backward.



TEXT-FIG. 8. Left anterior lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34113, locality C; $\times 2.1$. B, *Baringaspis dineleyi* Miles, after Miles 1973, text-fig. 4; $\times 1.4$. C, *Heightingtonaspis anglica* (Traquair), after White 1969, text-fig. 33; $\times 1$. D, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 110H; $\times 2.1$.



TEXT-FIG. 9. Anterior paired plates of right side of venter. A, *Eskimaspis heintzi* gen. et sp. nov., restored after cast of 34123, locality A; $\times 1.4$. B, *Baringaspis dineleyi* Miles, restored after 34127, locality A; $\times 1.1$. C, *Heightingtonaspis anglica* (Traquair), modified from White 1969, text-fig. 35; $\times 1.1$. D, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 112H; $\times 1.3$. AV, antero-ventral; AVL, anterior ventro-lateral; IL, inter-lateral; SP, spinal; pf, pectoral fenestra.

The overlap areas on the anterior ventro-lateral plate (Pl. 80, fig. 10) suggest that the anterior medio-ventral plate is shorter than the posterior medio-ventral and the anterior ventro-lateral plate did not meet the posterior lateral plate.

The tubercles of the ornamentation in the anterior ventro-lateral plate tend to concentric arrangement, in the spinal plate they are enlarged, and flat-topped on the lateral margin.

The scapulocoracoid (Pl. 80, fig. 7) preserved on the visceral surface of the anterior ventral wall of the trunk armour is comparable with that of the *Kujdanowiaspis*. It consists of a coracoid and lateral process with grooves for cutaneous nerves and vessels.

The posterior ventro-lateral plate (Pl. 79, fig. 5; Pl. 80, fig. 4; text-fig. 10A) is closely similar to that of *Kujdanowiaspis* and *Baringaspis* in the subtriangular shape and proportional size.

The posterior medio-ventral plate (Pl. 80, fig. 12; text-fig. 11A) is remarkably long, with a narrow exposed surface ornamented with coarse tubercles. As in *Baringaspis* (Pl. 80, fig. 10; text-fig. 11C) the plate overlies the anterior medio-ventral.

The anterior medio-ventral plate has not yet been determined in the collection but, as said above, the adjacent plates suggest that it should be similar to that of *Baringaspis* (Pl. 80, fig. 8; text-fig. 11B), i.e. shorter than the posterior.

The overlap between the two medio-ventral plates is in a few instances known in dolichothoracans. Nevertheless, the genera well known in this aspect show that the longer of the two plates usually overlies the shorter. The present anterior plate is longer and overlies the posterior such as in *Bryantolepis* (Denison 1958, fig. 113C) and *Anarthraspis* (Denison 1958, fig. 113D), conversely the longer posterior overlies the anterior in *Eskimaspis*, *Baringaspis* as well as '*Phlyctaenaspis*' (Denison 1958, fig. 113A), and *Phlyctaenaspis* (Denison 1958, fig. 113B).

Posterior median plates. Three detached plates behind the trunk armour occur in the collection. They are symmetric, strongly arched, from 16 to 18 mm in length. Two of them are suboval in shape, with a blunt anterior end. The third differs in having a deep slot in its anterior half. Their ornamentation of scattered tubercles is similar to that of the armour of *Eskimaspis*. In his paper Miles described some disarticulated plates in the Peel Sound Formation as posterior medians of *Baringaspis*. Of them, the one figured (Miles 1973, pl. 13, fig. 2) shows ornamentation identical to that of *Eskimaspis* rather than to that of *Baringaspis*, but it is much larger and broader than the plates mentioned above. Though similar plates behind the trunk armour were found in both dorsal and ventral midlines of the body in the well-preserved *Sigaspis* (Goujet 1973), the three plates in the collection are assumed to be dorsals because of their great convexity.

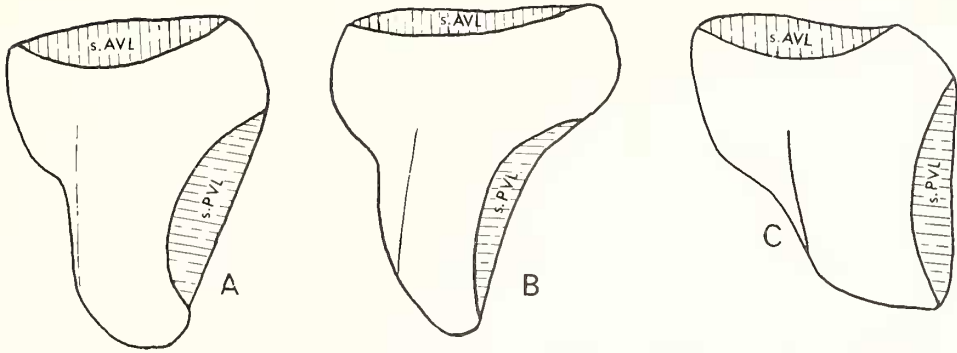
The age of the fish-bearing beds. The following vertebrates are associated with the arthrodires from the Peel Sound Formation south of Baring Channel.

	Location A	Location B	Location C
<i>Ctenaspis russelli</i> Dineley			X
<i>Escharaspis alata</i> Elliott			X
<i>Poraspis</i> sp.	X		
<i>Stegobrachiaspis baringensis</i> Elliott	X	X	X
<i>Weigeltaspis</i> sp.	X		
<i>Cephalaspis</i> sp.	X		
<i>Acanthodii</i> indet.	X	X	X
Poraspididae indet.	X	X	
Pteraspididae indet.	X		
<i>Crossopterygii</i> indet.	X	X	X

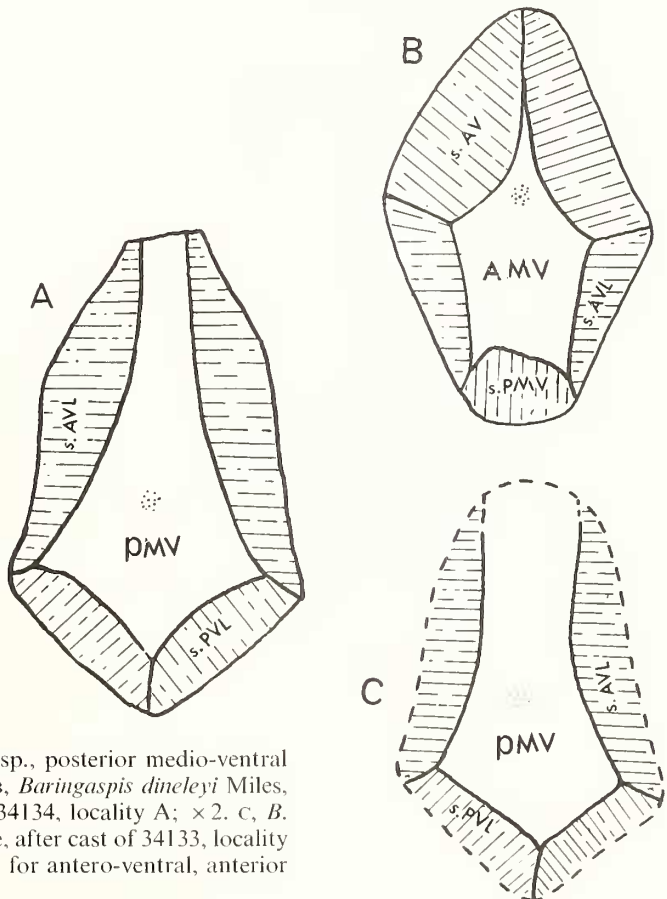
Elliott (1983) concluded that an age equivalent to the *crouchi* zone of the Anglo-Welsh succession (late Gedinnian) is probable on the basis of the fossils listed here.

As described above, *Eskimaspis* in many ways retains the primitive conditions proposed by Denison (Denison 1958, pp. 543-545) for dolichothoracans; in particular it approaches *Kujdanowiaspis* and *Heightingtonaspis* from the 'Old Red' Dnestrov Series of Podolia and the Dittonian of Britain respectively (Denison 1958, p. 500). Furthermore, together with *Baringaspis* and *Eskimaspis* occurs *Poraspis* sp. closely similar to *P. sericea* from the middle Dittonian of Britain. This tends to add weight to the opinion (Elliott 1983) that this part of the Peel Sound Formation is of middle Dittonian age which equates with the upper Gedinnian of the Rhenish facies.

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TEXT-FIG. 10. Right posterior ventro-lateral plates. A, *Eskimaspis heintzi* gen. et sp. nov., after cast of 34116, locality A; $\times 1.7$. B, *Baringaspis dineleyi* Miles, after cast of 13243, in Miles 1973, pl. 14, fig. 2; $\times 1.3$. C, *Kujdanowiaspis* sp., after Denison 1958, text-fig. 114r; $\times 1.8$. s.AVL, s.PVL, overlap areas for anterior ventro-lateral, posterior ventro-lateral.



TEXT-FIG. 11. A, *Eskimaspis heintzi* gen. et sp., posterior medio-ventral plate, after cast of 34139, locality A; $\times 2$. B, *Baringaspis dineleyi* Miles, anterior medio-ventral plate, after cast of 34134, locality A; $\times 2$. C, *B. dineleyi* Miles, posterior medio-ventral plate, after cast of 34133, locality A; $\times 2$. s.AV, s.AVL, s.PMV, s.PVL, areas for antero-ventral, anterior ventro-lateral, posterior medio-ventral.

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D. L. DINELEY

Department of Geology
University of Bristol
Bristol BS8 1TR

LIU YUHAI

Institute of Vertebrate Palaeontology and Palaeoanthropology
Beijing
People's Republic of China